The Nesting Biology of Three Species of *Hoplitis* Klug

(Hymenoptera: Megachilidae)

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Trapnesting studies conducted in Yellowstone and Grand Teton National Parks, Wyoming, and Lake, Napa, Solano, and San Joaquin counties in California (Table 1) have produced new or supplementary information on the nesting biology of four Nearctic species of *Hoplitis* Klug. Nests from the Grand Teton National Park area were given to us by Professor Howard E. Evans of Colorado State University. Evans used trapnesting techniques described by Krombein (1967). Elderberry (*Sambucus*) stems were used at the other study sites in accordance with techniques described and used by Parker and Bohart (1966, 1968).

This paper contains information on the nesting biology of *Hoplitis hypocrita* (Cockerell), *H. fulgida fulgida* (Cresson), *H. fulgida platyura* (Cockerell), and *H. sambuci* Titus and discusses those nest features which can be used to biologically separate these taxa. Thorp (1969), Torchio (1974), and Parker (1975) have demonstrated the use of certain nest features in distinguishing some groups of bees and we have employed, in part, the format developed by them in presenting and comparing the biologies of the three species discussed in this paper. The nesting biology of a fourth species, *Hoplitis* (*Formicapis*) *robusta* (Nylander), has been discussed elsewhere (Clement and Rust, 1975).

Study Areas

Trapnesting studies were conducted at a site (elevation 2,395 m) about 0.6 km west of West Thumb, Yellowstone National Park, Wyoming. Drilled elderberry stems were randomly placed around the periphery of a small clearing (18 × 27 m) in the predominantly Lodgepole Pine, *Pinus contorta latifolia* Critchfield, forest. Interspersed with the Lodgepole Pine were fewer numbers of Subalpine Fir, *Abies lasiocarpa* (Hook.), and Englemann Spruce, *Picea engelmannii* Parry ex Engelm. Dominant plants in bloom during the period the trap nests

THE PAN-PACIFIC ENTOMOLOGIST 52: 110–119. APRIL 1976

were in place include: *Eriophyllum integrifolium* (Hook.), *Trifolium longipes* Nutt., *Cirsium foliosum* (Hook.), *Campanula rotundifolia* L., *Lupinus* spp., *Eriogonum* spp., and *Castilleja* sp.

Professor Evans conducted his studies (Evans, 1973) along Pilgrim Creek in the Teton National Forest, Wyoming, and near the Jackson Hole Biological Research Station in Grand Teton National Park, Wyoming. The elevation of both study sites is about 2,077 m. The landscape in both areas is dominated by large open meadows which support numerous species of wild flowers, and groves of Lodgepole Pine and Quaking Aspen, *Populus tremuloides* Michx.

California study areas 1 through 5 (Table 1) were located in a Hard Chaparral community characterized by *Adenostoma fasciculatum* H. & A., *Rhamnus californica* Esch., *Heteromeles arbutifolia* M. Roem., *Ceanothus* spp., *Quercus* spp., and *Pinus sabiniana* Dougl. Study areas 6 and 7 (Table 1) were located in the Foothill Woodland plant community. The dominant trees and shrubs in both areas are *Quercus douglasii* H. & A., *Quercus wislizensii* A. DC., *Umbellularia californica* (H. & A.), *Ceanothus* spp., and *Rhus diversiloba* T. & G. Average annual rainfall is below 64 cm in the Hard Chaparral community and below 103 cm in the Foothill Woodland community (Munz and Keck, 1959). Trapnests were mostly placed on easterly facing slopes.

HOPLITIS HYPOCRITA

Hicks (1926) published a note on nests of this species taken near Boulder, Colorado. We have examined fifteen nests from five study sites in California (Table 1).

Nest Architecture.—Nests were obtained from vertically placed and drilled elderberry stems with initial burrow diameters of 5–6 mm. The number of cells per nest ranged from 3–11 with longer burrows (range 74–220 mm) containing more cells. The linearly arranged elliptical cells (Fig. 1) exhibited middle diameters of 6.5–7.0 mm with anterior and posterior ends narrowing to 5–6 mm. Female bees carved the smooth walled cells out of the pithy portion of the stems. Nineteen female cells averaged 13.5 mm in length (range 11.5–14.5 mm) and fourteen male cells averaged 12.8 mm in length (range 11.8–14.0 mm).

Cells were separated by a double partition of masticated plant material, each partition 0.2–0.6 mm thick at the center. Anteriorly, partitions were noticeably concave with forward extending lateral margins well-attached to the burrow wall. Posterior surfaces were flat and rougher in texture. Numerous small pieces of pith taken

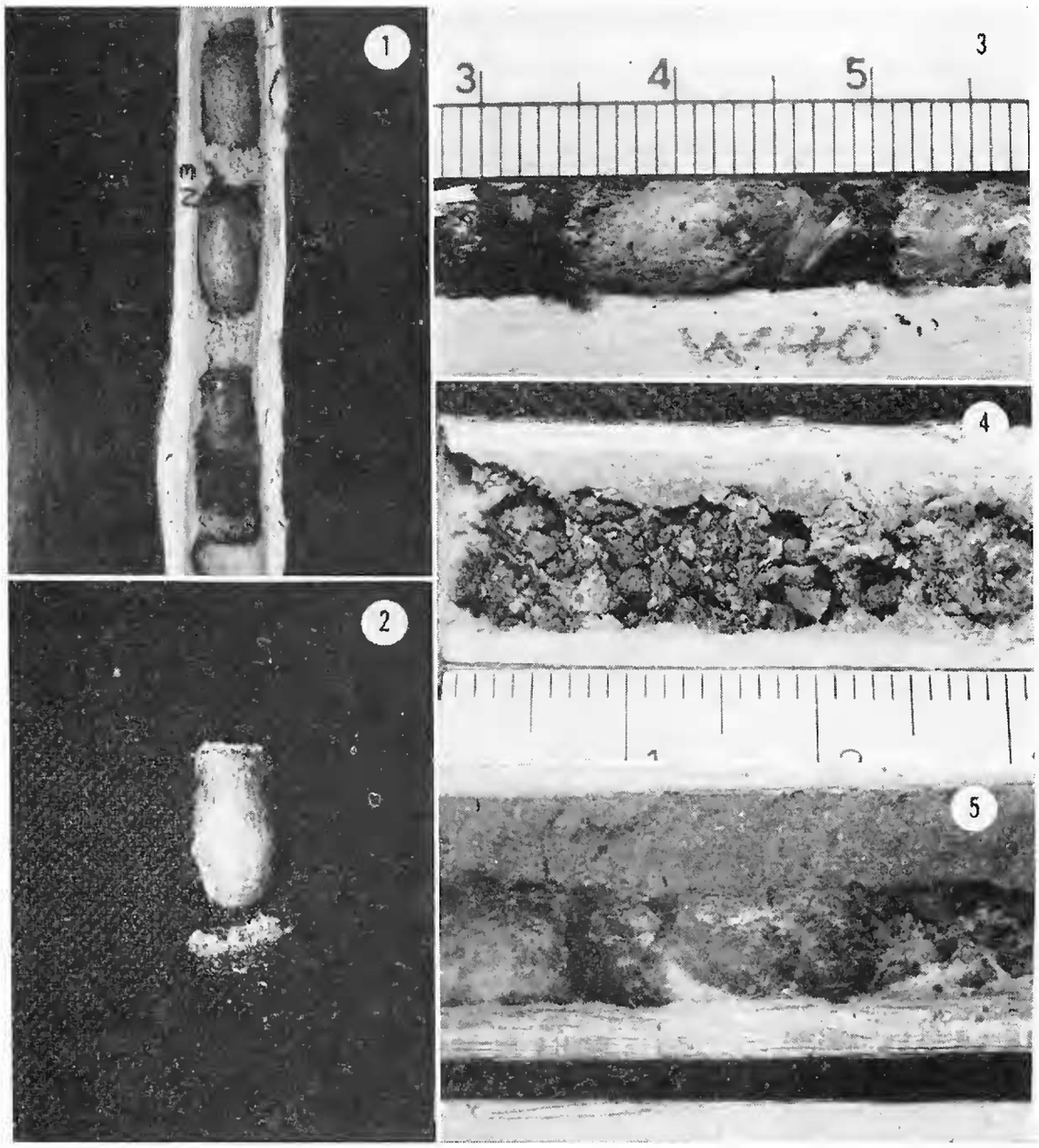
Table 1. Location and dates of study and number of *Hoplitis* trap nests recovered.

Study areas and dates of study	Species of *Hoplitis*		
	hypocrita	*fulgida*	*sambuci*
1. 2.4 km SE Nichilini Winery, Napa Co., CA. 1973.	6	–	2
2. 16 km N Pope Valley, Napa Co., CA. 1971–73.	1	2	11
3. 1.6 km SW Monticello Dam, Napa Co., CA. 1968.	–	2	8
4. 4.8 km SE Pope Valley, Napa Co., CA. 1971–73.	4	1	–
5. 3.5 km SW Cobb Mt. Lodge, Lake Co., CA. 1967.	–	–	7
6. 22.4 km SW Tracy, San Joaquin Co., CA. 1968.	2	–	–
7. 12.8 km SW Winters, Solano Co., CA. 1970.	2	–	–
8. West Thumb, Yellowstone National Park, WY. 1971.	–	1	–
9. Pilgrim Creek, Teton National Forest, WY. 1971.	–	1	–
10. Jackson Hole Research Station, Grand Teton National Park, WY. 1971.	–	6	–

from the burrow wall were tightly packed in between the two cell partitions (Fig. 1). Cellular partitions with pith pieces interposed filled intercellular connecting burrows ranging from 5–6 mm in diameter to 1–13 mm in length. The female bee placed a single thin layer (about 0.2 mm thick) of masticated plant material at the extreme posterior end of the burrow before carving out her first cell.

Nest plugs were usually constructed of two to five layers (0.2–0.8 mm thick) of masticated plant material with small bits of pith interposed. These plugs averaged 8.4 mm in length (range 5–13 mm). Female bees widened, to about 8 mm at the widest point, a section (range 5–15 mm in length) of the burrow between the burrow orifice and the outer-most layer of the nest plug, using the excess pith in construction of the nest plug. No vestibular cells were observed in any of the nests we examined.

Provisions and Development.—The dark brown provisions were



FIGS. 1–5. Nesting biology of *Hoplitis* species: Fig. 1—Portion of a *Hoplitis hypocrita* trap nest, the bottom cell contains a cocoon of the parasitic bee, *Stelis* sp. Fig. 2—A cocoon of *Hoplitis hypocrita* separated from anterior collar and fecal pack. Fig. 3—Portion of a *Hoplitis fulgida* trap nest. Fig. 4—Nest plug of a *Hoplitis fulgida* trap nest. Fig. 5—A cocoon of *Hoplitis sambuci in situ* separated from anterior collar and fecal pack.

moist and tacky but retained their original shape when removed from the cells. The shape and size of the pollen stores was somewhat variable but most were nearly cylindrical in cross section (range 4–5 mm) along their entire length (range 4.0–7.5 mm). Provisions generally filled a little more than the bottom half of a cell. A layer of dry yellow pollen covered the lower portions of the provisions and presumably served to prohibit them from contacting the basal cell partitions.

From the location of several dead eggs, it appears that an egg is deposited on a median lobe which projects slightly from the oblique outer surface of the provisions. Microscopic examination of pollen taken from several cells revealed that female bees relied almost exclusively on leguminous pollen.

The dark brown to reddish-orange fecal pellets were evenly rounded at both ends and varied from 0.2–0.25 mm in width to 0.7–1.0 mm in length. We observed a shallow, longitudinal, groove about 0.07 mm wide in most of the pellets. Larvae incorporated most of the pellets into a separately woven cocoon which formed an anterior collar (range 2–5 mm in length) over the main cocoon (Fig. 2). Smaller amounts of feces were woven into the main cocoon and smeared against cell walls and basal cell partitions.

The anterior collar is composed of a clear matrix intermixed with fine silk threads. It is firmly attached to the cell cap and is connected to the anterior nipple of the cocoon by a concentrated network of silk threads. The non-elevated nipple is composed of a dense mat of white silk threads about 1.5 mm in diameter and is visible from both outer and inner surfaces of the cocoon. Anterior collars do not possess distinct anterior nipples.

The cocoon fills the cell and conforms to the shape of the cell. It is usually thinner than the collar and translucent; basically constructed of a single salivary matrix with white silk threads interwoven. In some cases, a loose network of fine silk threads covered the entire outer cocoon surface.

Hoplitis hypocrita overwinter as postdefecating larvae.

Associates.—We recovered an unidentified species of *Stelis* from four nests in study area 1.

HOPLITIS FULGIDA

Two nests of *H. fulgida* from Colorado were described by Hicks (1926) and his notes are the only published information on this species. We have examined thirteen nests of this species; five nests of *H. fulgida platyura* from two locations in California and eight nests of the nominate *H. fulgida* from the Grand Teton Park area and Yellowstone National Park, Wyoming (Table 1). We have been unable to detect any differences in the nesting biology of the subspecies. The biology of both is combined into one discussion.

Nest Architecture.—Seven nests obtained from the Grand Teton area were in drilled pine blocks (2.5 × 15.2 cm) with burrow lengths ranging from 123–133 mm and diameters of 4–5 mm. The other six

nests were in drilled elderberry stems with initial burrow diameters of 5–6 mm; burrow lengths varied from 62–300 mm.

The number of cells per nest averaged 5.1 (range 1–10). The first cell of a linear series is constructed in the bottom of the burrow. Seventeen male cells averaged 9.2 mm (range 8–11 mm) and twelve female cells averaged 9.4 mm (range 7–12 mm) in length.

The cell partitions were composed of two layers (Fig. 3) of masticated leaf material and small pebbles and/or wood chips. Partitions varied from 0.3–2.0 mm in thickness at the center but they were similar in shape to *H. hypocrita* partitions. In elderberry stick-traps the female bees packed small pith pieces taken from the burrow wall into the space between the two partitions, whereas in pine block stick-traps the gap was usually filled with small pebbles, pieces of pine needles, and wood chips (Fig. 3). The intercellular partitions plus the interposed material filled a distance of 3–10 mm in the nests we observed. Intercalary cells were noted between two provisioned cells in each of two nests from the Grand Teton area. These cells measured 13 and 22 mm in length and contained small, evenly distributed, amounts of wood chips and dirt pebbles.

An undivided vestibular cell averaging 25.1 mm (range 11–50 mm) extended anteriorly from the last provisioned cell to the nest plug in nine of the nests we studied. Within vestibules, we found small amounts of vegetative parts and dirt pebbles lightly packed against the outer surface of the last cell partition. The nest plug was flush with the last provisioned cell in the remaining four nests.

Nest plugs were located an average of 11.3 mm (range 5–27 mm) inside of the burrow orifice. In most nests the plugs were composed of the last cell cap and an outer, slightly thicker (range 1–3 mm thick), layer of masticated green plant material. The space between the partitions was usually tightly filled with the same type of material found in the vestibular cells. Double layered nest plugs averaged 5.3 mm in total length (range 3–9 mm). In two instances where vestibular cells were absent, the nest plugs contained 3 and 4 separate partitions anterior to the last cell cap (Fig. 4). These nest plugs were 16 and 21 mm in length.

Provisions and Development.—Provisions were not recovered and thus we have no information on the nature of the pollen-nectar stores and the placement of eggs.

The red-orange to black fecal pellets ranged in size from 0.2–0.3 mm in width and 0.5–0.9 mm in length. Most were slightly curved with rounded ends and without grooves. In most cases, a majority of the

pellets were packed into the anterior end of the cells and held in place by an anterior collar-like cocoon (Fig. 3). This collar covered 1–3 mm of the main cocoon which was slightly smaller in size than the cell. Some fecal pellets were incorporated into the cocoon, smeared into the side walls of the cell, and scattered loosely around edges of the cell.

There appears to be some variation in cocoon construction since a few larvae did not spin an anterior collar. When present, a collar was composed of a clear matrix with silk threads interwoven. Cocoons were of similar construction but were usually more pliable and transparent. Outer collars were attached to the anterior nipple of a cocoon. A dense network of silk fibers formed the slightly elevated nipple of a cocoon; anterior collars did not have nipples. A loose network of silk threads covered portions of the outer surface of a few cocoons.

This species overwinters in the postdefecating larval stage.

Associates.—Three parasites were reared from the Grand Teton nests: the eulophid parasite, *Melittobia* sp., *Sapygia aculeata* Cresson, and *Stelis* sp.

HOPLITIS SAMBUCI

There are no published accounts on the nest architecture, provisions, and the development of this species. Twenty-eight nests of *H. sambuci* were recovered from four California study sites (Table 1).

Nest Architecture.—The nests were obtained from drilled elderberry stems with initial burrow diameters of 4.5–6.0 mm. Burrow lengths averaged 117 mm (range 74–210 mm). The linear celled nests had an average of 5.4 cells (range 2–10 cells) and the first cell in a series was placed at the extreme posterior end of the burrow. Twenty-five female cells averaged 11.64 mm in length (range 9.5–13.0 mm) and forty-two male cells averaged 9.55 mm in length (8–11 mm).

The cells were separated by a single or a double partition composed of small brittle pieces of yellow or dark green to black masticated plant material and embedded bits of pith. The dark green plant tissue was noticeably covered with epidermal hairs, giving these partitions a rough and hairy appearance. Between double partitions a space 1–2 mm long was filled with pithy sawdust taken from the burrow wall. The partitions were 0.3–0.8 mm thick at the center and were similar in shape to those of *H. hypocrita* and *H. fulgida*. We found both single and double cell partitions within a single linear cell series.

The nest plugs were located within the burrow and adjacent to the last cell. However, in one nest where *H. sambuci* had superceded a *Trypoxylon* wasp, we discovered an open vestibular cell 22 mm in

length. The plugs averaged 10 mm in length (range 6–25 mm) and were composed of 4–10 alternating layers of masticated plant material and elderberry pith pieces. Nest and cell partitions were similar in shape and construction.

Provisions and Development.—The light yellow provisions were placed flush against posterior cell partitions. The smooth surfaced provisions were of a spherical shape and usually filled the bottom one-half of a cell. The mixture was dough-like and slightly moist and a layer of dry yellow pollen coated most of the outer surface. Five pollen-nectar balls each produced a dead egg from a small shallow pocket on their outer surface. We were unable to identify the pollen source.

Feces varied from light yellow to dark brown in color. The cylindrical pellets were rounded at the ends and 0.2–0.3 mm wide and 0.5–0.7 mm long. We detected no grooves or ridges. Most of the pellets were packed in the anterior end of the cell (Fig. 5). Smaller amounts were incorporated into the cocoon and some were scattered loosely around the edge of the cell.

In a fashion similar to what we observed in *H. hypocrita* cells and most *H. fulgida* cells, the anteriorly packed fecal pellets were held in place by a separately woven anterior collar (Fig. 5). This collar was 0.8–2.0 mm in length and was composed of a thin cellophane-like material with silk threads interwoven. It was connected to the main cocoon by a sparse network of silk threads but the two were easily separated. The anterior collar and attached fecal pack were firmly connected to the cell cap (Fig. 5).

Incorporated into the single parchment-like layer of the main cocoon were numerous silk threads. The layer was also noticeably stained with feces. Inner surfaces were smooth and outer surfaces were covered with a loose but fairly dense network of fine silk threads. Anterior nipples were not detected. The cocoon fills the cell and conforms to the shape of the cell.

Hoplitis sambuci overwinter as postdefecating larvae.

Associates.—Two nests from study area 2 each produced a meloid larva and one nest from the same locality produced the parasitic bee, *Stelis* sp.

SUMMARY

We were able to reliably differentiate nests of the three species discussed in this paper. Nest features which appear to be of diagnostic value include: cell shape and size; nature of the plant material used in partition construction; type of material (when present) combined

Table 2. Comparisons of eleven nest characteristics between four species of North American *Hoplitis*.

Nest Characteristic	Species of *Hoplitis*			
	hypocrita	*fulgida*	*sambuci*	*robusta*[1]
1. Cell shape cylindrical (+), elliptical (—).	—	+	+	+
2. Cell partitions double layered with interposed material (+), single layered (—).	+	+	±	—
3. Partitions composed only of masticated plant material (+), other material added (—).	+	—	—	±
4. Nest plugs inside of burrow orifice.	+	+	+	—
5. Vestibular cells present.	—	±	±	±
6. Intercalary cells present.	—	±	—	—
7. Provisions cylindrical in cross section.	±	?	+	+
8. Egg deposited on oblique surface of provision on median lobe (+), in pocket on rounded surface (—).	+	?	—	—
9. Feces mostly packed in anterior end of cell.	+	+	+	—
10. Cocoon covered anteriorly by separately woven collar-like cocoon with feces attached.	+	±	+	—
11. Nipple present on cocoon.	+	+	—	—

[1] Data from Clement and Rust (1975).

with masticated plant material to form partitions; nature of the material interposed between partitions; shape of the pollen-nectar provisions; position of the egg; presence or absence of a nipple on the cocoon; and presence or absence of a separately woven collar covering anterior portions of the cocoon. A comparison of a few neutral and the more visible diagnostic characters are summarized in Table 2.

When bee biologists have added to the existing biological information available on the genus *Hoplitis* then perhaps it may be possible to demonstrate a biological separation of most of the species. Especially needed are detailed studies describing the nest architecture, provisions and development of individual species. Eickwort (1973) has published

the most thorough biological account of a species of *Hoplitis* found in the Nearctic.

ACKNOWLEDGMENTS

We would like to thank H. E. Evans for providing us with the Grand Teton material and D. S. Horning for the loan of some material from San Joaquin, Napa, and Lake Counties in California. Mr. B. Villegas kindly identified the *Sapygia* species. Authorities from Grand Teton and Yellowstone National Parks gave permission to Professor Evans and the co-author (S.L.C.) to undertake stick-trap studies in these parks.

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